REPRODUCTION OF SOME DEMOSPONGES IN A TEMPERATE AUSTRALIAN SHALLOW WATER HABITAT

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Species of *Tethya, Chondrilla, Mycale* and *Echinodictyum* were monitored for two years at South Mole, Fremantle, Western Australia (32°04'S, 115°45'E) to determine onset of reproductive activity, sex phenotype, and reproductive mode. Most reproductive activity occurred from late spring through summer and autumn (November-April). Most species appear to be gonochoric with both ovipary and vivipary recorded. Details of their reproductive development is reported and discussed in relation to sea temperature data. ❐ *Porifera, Demosponges, Fremantle, Western Australia, reproduction.*

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The only previous study on the reproductive biology of temperate Australian marine demosponges (Hoskins, 1992), found low numbers of oocytes present between March and September in populations of *Phyllospongia* sp. from Rottnest Island, Western Australia (WA). This lack of basic biological information for this region is surprising given that sponges are a dominant component of the sessile fauna in these temperate marine habitats. Consequently, the present study aimed to collect baseline reproductive data for some of the more common species of demosponges in this region, examining species of *Echinodictyum, Mycale, Haliclona, Coelosphaera, Tethya* and *Chondrilla.* Both *Tethya* and *Chondrilla* have two distinctive colour morphs at the study site, possibly indicating sympatric species, so these colour morphs were monitored as separate populations.

Several studies undertaken in Europe and USA have described reproductive characteristics for temperate species belonging to some of the genera examined here. For instance, Elvin (1976) reported on the reproductive biology of *Haliclona permollis* in Oregon; Fell (1976) on *H. loosanoffi* in Connecticut; and Wapstra & Van Soest (1987) on *H. oculata* and *H. xena* in Holland. *Mycale micracanthoxea* from Holland (Wapstra & Van Soest, 1987) is the only temperate species of *Mycale* previously examined. Temperate populations of *Chondrilla nucula, Tethya aurantium* and *T. citrina* were studied by Liaci (1971a, b), whereas there are no published studies on the reproductive biology of *Coelosphaera* or *Echinodictyum*.

Increasing temperature is generally accepted as a major environmental factor regulating the onset of reproductive activity in sponges occurring in regions of large seasonal change (Fell, 1983; Simpson, 1984). Only four species are presently known where gametogenesis is associated with a decrease in temperature: *Halisarca dujardini* (Lévi, 1956; Chen, 1976) *Desmacidon fructicosum* (Lévi, 1956), *Tethya crypta* and *Aplysina gigantea* (Reiswig, 1973). In this study seasonal reproductive activity is discussed in relation to sea temperature data, and results are presented on the mode of reproduction and sexual phenotype of the species examined, estimates of development time of gametes, and timing of product release.

MATERIALS AND METHODS

The six species of sponges investigated here live subtidally on the ocean side of South Mole, an artificial groyne that forms the southern flank of the entrance to Fremantle Harbour (32°04'S, 115°45'E). All six species at this site ranged in abundance from common to abundant (i.e. ≥10 specimens of each species seen during a dive of 1 hour duration). Sponges were prolific from 4-7.5m depth, occurring between the shallow seaweed (*Ecklonia*) fringe found at 0-4m depth and the sand flat with seagrass at the base of the groyne.

Sampling was conducted over two years from October 1996 to April 1998. Sampling ceased in

TABLE 1. Reproductive activity of the species studied at South Mole. Key: -, not sampled; NR, not reproductive; X, not found in the field; O, oocytes; E, embryos; L, larvae; S, sperm; (sample size).

Species (year of survey)	Month								
	A	S	O	N	D	J	F	M	A
Echinodictyum clathrioides (96-97)	- (0)	- (0)	NR (3)	- (0)	NR (2)	NR (3)	NR (4)	NR (2)	X (0)
Echinodictyum clathrioides (97-98)	X (0)	- (0)	NR (4)	NR (5)	NR (3)	NR (4)	O (4)	NR (3)	NR (4)
Coelosphaera sp. (96-97)	- (0)	- (0)	NR (2)	- (0)	NR (2)	NR (2)	NR (6)	NR (2)	OE (2)
Coelosphaera sp. (97-98)	NR (2)	- (0)	NR (3)	NR (3)	NR (3)	NR (3)	NR (3)	NR (3)	S (3)
Haliclona sp. (96-97)	- (0)	- (0)	X (0)	- (0)	NR (4)	NR (6)	X (0)	X (0)	NR (2)
Haliclona sp. (97-98)	EL (2)	- (0)	NR (2)	NR (4)	NR (4)	NR (4)	NR (3)	O (3)	S (4)
Mycale sp. (96-97)	- (0)	- (0)	NR (2)	- (0)	OELS (5)	ES (7)	NR (3)	NR (2)	NR (2)
Mycale sp. (97-98)	NR (2)	- (0)	NR (4)	S (6)	ELS (3)	ELS (5)	NR (4)	NR (2)	NR (4)
Chondrilla australiensis (ochre morph) (96-97)	- (0)	- (0)	NR (2)	- (0)	NR (2)	NR (5)	O (4)	NR (5)	NR (3)
Chondrilla australiensis (ochre morph) (97-98)	NR (2)	- (0)	NR (4)	NR (9)	NR (7)	NR (7)	O (6)	NR (2)	NR (2)
Chondrilla australiensis (maroon morph) (96-97)	- (0)	- (0)	NR (2)	- (0)	NR (4)	NR (2)	O (3)	X (0)	NR (4)
Chondrilla australiensis (maroon morph) (97-98)	NR (2)	- (0)	NR (2)	NR (2)	NR (2)	NR (4)	O (4)	NR (3)	NR (7)
Tethya sp. (pink morph) (96-97)	- (0)	- (0)	NR (2)	- (0)	X (0)	O (2)	O (4)	X (0)	NR (2)
Tethya sp. (pink morph) (97-98)	X (0)	- (0)	X (0)	NR (4)	O (10)	NR (9)	O (7)	O (9)	NR (8)
Tethya sp. (orange morph) (96-97)	- (0)	- (0)	X (0)	- (0)	NR (4)	O (4)	O (4)	O (5)	NR (2)
Tethya sp. (orange morph) (97-98)	NR (4)	- (0)	NR (7)	NR (5)	O (8)	O (6)	O (8)	O (10)	NR (9)

the winter months of May, June and July 1997 and no sampling was possible in November 1996 and September 1997 due to bad weather and sea conditions. From October 1996 to April 1997 monthly samples of random individuals of each species were collected. With the resumption of sampling in August 1997 two regimes were adopted: sampling of random individuals as for the previous season, and sampling of known individuals of each species to monitor for sequential hermaphroditism. Two different techniques were used. Specimens of *Tethya* were sampled with a 0.5mm diameter cork borer, and ramose branching, encrusting, massive and fan shaped species had a small piece incised from them with a scalpel. Numbers of specimens of each species that were collected and examined by light microscopy are indicated in Table 1.

After collection, individual samples were placed in labelled glass vials and on return to the laboratory were fixed in a gonad fixative, FAACC (100ml = 10ml 37-40% formaldehyde solution: 5ml glacial acetic acid: 1.3gm calcium chloride dihydrate: 85ml tap water) for ≤48 hours, and then transferred to 75% ethanol. Sections cut at 8μm were stained with haematoxylin-eosin, mounted, and surveyed by light microscope for presence and development of eggs and sperm.

Average sizes of gametes were calculated, using an ocular micrometer, by measuring gametes from each gravid individual for each sampling period. To decrease sampling variation only oocytes sectioned through the nucleus, and sperm cysts sectioned through the midline, were measured.

Temperatures at 7m depth adjacent to the Fisheries Western Australia Marine Research Laboratories at Waterman were recorded twice daily (M. Rossbach, Fisheries Western Australia, pers.comm.). Monthly averages of this data, supplied by Fisheries WA, were calculated for the sampling months outlined above.

RESULTS

1. *Echinodictyum clathrioides* Hentschel, 1911 (Poecilosclerida: Raspailiidae). Adults of *E. clathrioides* are erect, fan shaped individuals that are at least 30cm in diameter. Female gametes were only found in specimens collected in February 1998, when oocytes were 45µm diameter (Fig. 1A). There were no oocytes in either January or March suggesting rapid oocyte development and release of products (Table 1). Small sponges ≤8cm diameter were found in April 1998.

2. *Coelosphaera* sp. (Poecilosclerida: Coelosphaeridae). Individuals of this species are rounded mounds with apical oscules and are bright orange alive. Reproductive products were found in April of both sampling seasons (Table 1). Oocytes and embryos (Fig. 1B) were present in April 1997 and sperm in April 1998 implying that reproductive development of embryos and larvae occurs in autumn and possibly winter.

3. *Haliclona* sp. (Haplosclerida: Chalinidae) is a maroon, ramose branching sponge with apical oscules. Specimens of this species rarely had reproductive products during this sampling program. Large embryos and larvae (Fig. 1C) were present in August 1997, and developing oocytes were found in March and sperm in April 1998 (Table 1). Presence of gametes at this time suggest that this species is reproductively active throughout winter. This species is viviparous and individuals are either gonochoric or successive hermaphrodites.

4. *Mycale* sp. (Poecilosclerida: Mycalidae). This species exudes large amounts of mucous upon collection. In the field the sponge has short, thick erect lobes with prominent conules, and is irridescent mauve or vivid blue. Sampling of the mesohyl of this species for reproductive products was difficult as most of the mesohyl oozed away prior to the sponge being placed in the collection vial, and the mesohyl that remained was detached from the skeleton prior to fixation. However, this species has particularly obvious and abundant female gametes visible in the field as orange spheres of about 2mm diameter. Because of the mucous mesohyl, few of these products were successfully sectioned. Female gametes were found in the field during December and January in 1997 and 1998, and were absent in February of both years (Table 1). Sperm cysts were found interspersed amongst embryos and larvae (Fig. 1F). Reproductive activity occurred for a minimum period of 62 days from first development noted in November to the last date when gametes were present in January. This species is viviparous and contemporaneously hermaphroditic.

Two colour morphs were observed in the remaining two genera examined, *Tethya* and *Chondrilla*. Consequently, replicate specimens of each morph were monitored separately to determine if reproductive timing or sex determination differed between them.

5. *Chondrilla australiensis* Carter, 1873 (Hadromerida: Chondrillidae). Specimens were either ochre to brown or maroon. The ochre colour morph was the dominant morph at the study site with extensive mats, up to 1m across, living in full light. Although both morphs tended to occur either in full light or shade under *Ecklonia*, the maroon morph occurred more frequently in shaded areas. Few reproductive products were found in either morphotype. Individuals were found with oocytes in late February 1997 (Table 1). No products were seen in the next sampling in late March. Oocytes measuring 30-40µm were abundant in February 1998 and had cellular extensions between the mesohyl and the oocytes (Fig. 1E). Oocyte development in this species is rapid with 34 days elapsing between the January sampling (when no female products were visible) and the February sampling (when oocytes were 30-40µm). No oocytes were present in the March sampling 21 days later. No sperm were seen in either sampling year. It is assumed therefore that spawning occurs in late February or early March, approximately 2-4 weeks earlier than in *Tethya*. These sponges are oviparous and probably gonochoric. Asexual reproduction by fragmentation appeared to be occurring in *C. australiensis* in April 1998, whereby elongated tear shaped droplets of sponge tissue were found extending from the edges of some of the adults. The tissue was thinnest at the point of attachment to the adult sponge and thickest at the furthest edge. It is likely that these droplets would detach from the adult and settle on the substrate beneath.

6. *Tethya* sp. (Hadromerida: Tethyidae). Specimens were either pink or orange and individuals of both colour morphs had numerous oocytes in February and March of 1997 and 1998. Oocyte development was first detected in early December when oocytes were 10-12µm in diameter. Ninety eight days later, in early March, oocytes were 50-70µm in diameter (Fig. 1D).

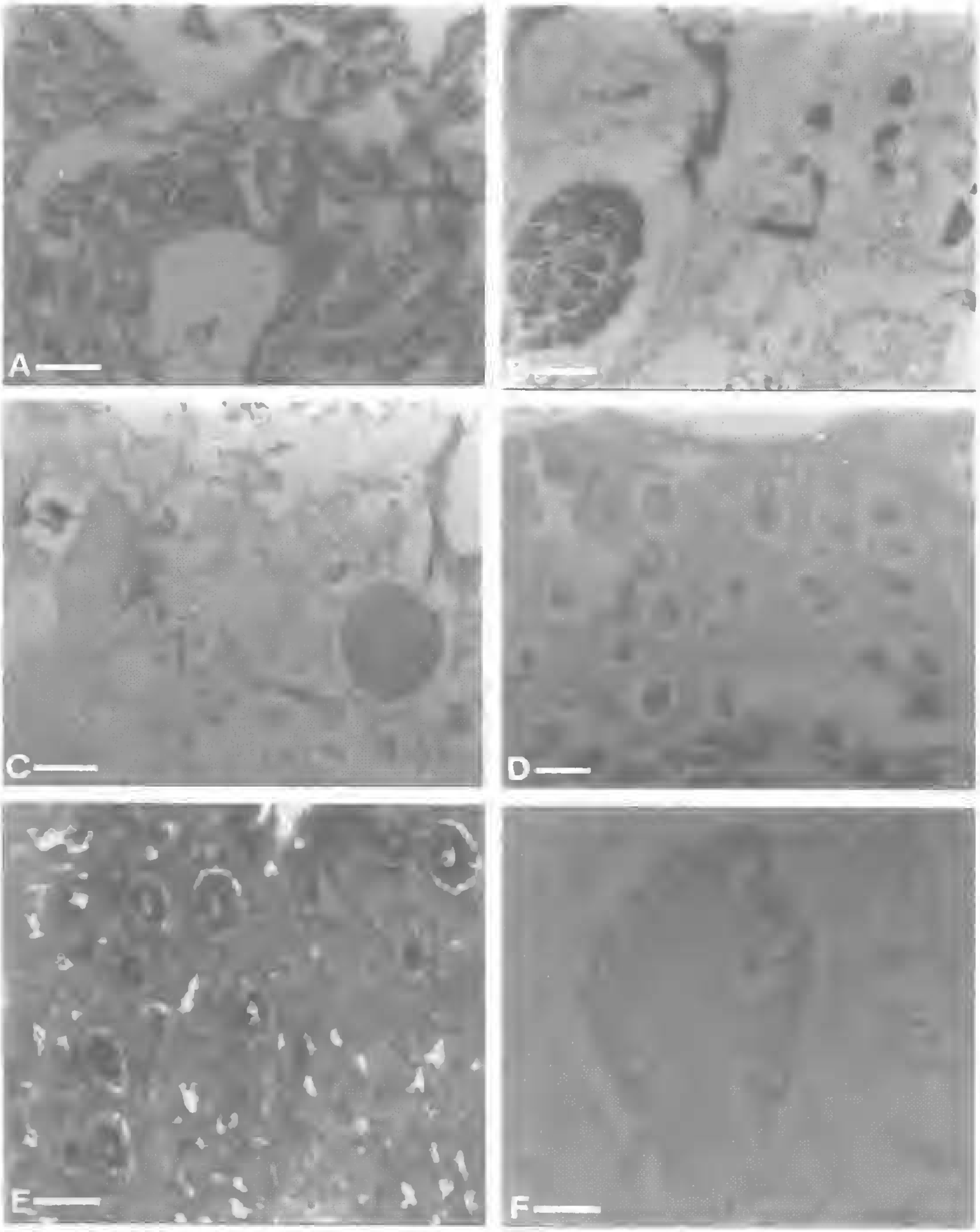

FIG. 1. Reproductive products of species examined in this study. A, Oocytes in *Echinodictyum clathrioides* 17/2/98. B, Embryo and oocytes in *Coelosphaera* sp. 29/4/97. C, Larvae and embryo in *Haliclona* sp. 26/8/97. D, Oocytes in *Tethya* sp. 25/3/97. E, Oocytes in *Chondrilla australiensis* 17/2/98. F, Larvae and sperm cysts (←) in *Mycale* sp. 20/12/96 (scale bar: E = 50μm, A-D, F = 100μm).

TABLE 2. Developmental mode of some sponge species in Western Australia. Abbreviations: X = developmental mode, ? = suspected developmental mode but awaits confirmation

Species	Ovipary	Vivipary	Gonochorism	Contemporaneous hermaphroditism	Successive hermaphroditism
Tethya sp.	X		?		
Chondrilla australiensis	X		?		
Echinodictyum clathrioides	?		?		
Mycale sp.		X		X	

There were no oocytes in samples taken at the next sampling period in April, either in 1997 or 1998 (Table 1). It is therefore likely that spawning occurs in mid to late March. No sperm were found in either sampling years. These sponges are oviparous and probably gonochoric. Thin filaments were seen extending from one individual of *Tethya sp.* in April 1998. This individual had been sexually reproductive with oocytes visible in March.

In summary, two types of reproductive mode were observed amongst these six species: ovipary in *Tethya* sp. and *Chondrilla australiensis*, and vivipary in *Mycale* sp., *Coelosphaera* sp. and *Haliclona* sp. (Table 2). Only one sex phenotype was determined, contemporaneous hermaphroditism was found in *Mycale* sp.

Two opposing trends are apparent when sea temperatures are compared with timing of reproductive activity (Fig. 2). In *Tethya* sp., *Chondrilla australiensis*, *Mycale* sp. and probably *Echinodictyum clathrioides* reproductive activity occurs in late spring or summer when sea temperatures are increasing or reaching a maximum. Conversely, in *Coelosphaera* sp. and *Haliclona* sp. reproductive activity occurs in autumn when sea temperatures are falling.

DISCUSSION

REPRODUCTIVE BIOLOGY. Sponges can be either gonochoric or hermaphroditic, oviparous or viviparous. In Haplosclerida both gonochorism and hermaphroditism have been reported, although all species examined to date have been viviparous. Tropical species of *Haliclona* from the Great Barrier Reef (*H. amboinensis* and *H. cymaeformis*; Fromont, 1994), and temperate intertidal species from the Oregon coast (*H. permollis*; Elvin, 1976), and from a Connecticut estuary (*H. loosanoffi*; Fell, 1976) are all viviparous and gonochoric. However, two species from a temperate European locality were reported as viviparous with contemporaneous hermaphroditism (Wapstra & Van Soest, 1987). In this study, *Haliclona* sp. is viviparous but is not contemporaneously hermaphroditic. This species is either gonochoric or a successive hermaphrodite.

Ilan & Loya (1990) reported finding aggregations of female reproductive products in species of the haplosclerid families Chalinidae and Niphatidae, and suggest these brooding chambers may be common amongst haplosclerids. In this study *Haliclona* sp. did not have brood chambers but had reproductive products aligned along the midline of the branches.

Mycale sp. conformed to previous reports of sex determination and reproductive mode for this genus, being viviparous and hermaphroditic. The temperate European species, *Mycale micracanthoxea*, the tropical Red Sea species, *M. fistulifera*, and *Mycale* sp. reported here are all viviparous and contemporaneous hermaphrodites (Wapstra & Van Soest, 1987, Meroz & Ilan, 1995, Reiswig, 1973).

There are no previous reports on mode of reproduction or sex determination in species of the genus *Coelosphaera* or *Echinodictyum*.

Chondrilla australiensis from South Mole was oviparous and probably gonochoric conforming to published reports of the reproductive biology of this genus. *Chondrilla nucula* from Italy has been reported to be oviparous and gonochoric (Liaci et al., 1971a).

Sponges possess high regenerative capacities and have been reported to reproduce asexually by budding, fragmentation and gemmulation (Fell, 1993). Fragmentation is possible because of the structural homogeneity and morphological flexibility of sponges so that even small fragments are likely to possess all essential functional elements and can readily reorganise to function as independent entities (Wulff, 1991). The droplets of tissue I found extending from the edges of some adults of *C. australiensis* in April 1998 appear to be a form of asexual reproduction through fragmentation.

In *Chondrilla nucula* cellular extensions between the mesohyl and oocytes are described as long thin filipodia connecting the nurse cells surrounding the developing eggs to the egg

A.

Species	Month								
	A	S	O	N	D	J	F	M	A
Tethya sp.					X	X	X	X	
Chondrilla australiensis							X		
Echinodictyum clathrioides							X		
Mycale sp.				X	X	X			
Coelosphaera sp.									X
Haliclona sp.	X							X	X

B.

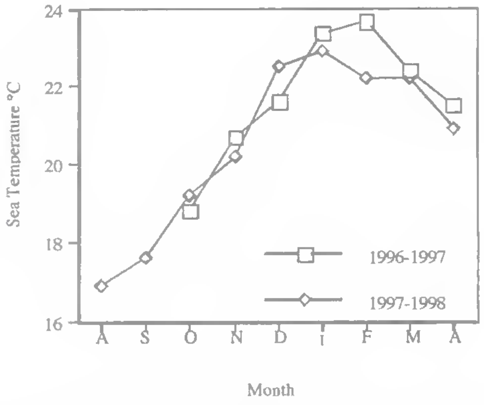

FIG. 2. Reproductive activity and sea temperature. A, Timing of reproductive activity. X = months when the species had reproductive products. B, Average monthly sea temperatures.

surfaces, and Liaci et al. (1971a) suggested that these connections allow a direct, nonphagocytic transfer of nutrients. Similarly, the cellular extensions I observed surrounding eggs in *Chondrilla australiensis* are likely to have the same function.

Tethya sp. individuals were oviparous and probably gonochoric, conforming to previous reports in the literature for both tropical species *T. crypta* (Reiswig, 1973), and temperate species *T. aurantium* and *T. citrina* (Liaci et al., 1971b).

Asexual budding has been reported for species of *Tethya*. Thin filaments containing spicules extend outwards from the adult and a spherical bud forms distally. This bud detaches from the adult and can attach to the substratum (Simpson, 1984). Thin filaments were seen extending from one individual of *Tethya* sp. in April 1998 but distal buds were not apparent at this time.

COLOUR VARIATION WITHIN SPECIES. *Chondrilla australiensis* and *Tethya* sp. each had two distinctive colour morphotypes at the study site. In *C. australiensis* the usual occurrence of the maroon morph in shaded or cave habitats suggests that its colour difference to the ochre morph, growing in full light, may be a response to reduced light conditions. The Northern hemisphere species *C. nucula* usually colonises illuminated bottoms and is generally brownish (Gaino et al., 1976). Arillo et al. (1993) found that its colouration is a consequence of the presence of the cyanobacteria *Aphanocapsa* sp. Similarly, it is speculated that colour differences between morphs at South Mole could be the result of either different cyanobacterial symbionts within the two morphs, or differing abundances of the symbionts in the two morphs. Individuals of both morphs occurred side by side with marked non-overlap zones between them. These zones were also common between specimens of the same colour morph, suggesting the occurrence of different genotypes within the same colour morphs, and that sexual reproduction is occurring to some extent in the population.

In *Tethya* sp. individuals of each colour morph occurred side by side in full light and under *Ecklonia*. Therefore, colour differences between the morphs cannot be attributed to differences in light regimes. The coexistence of more than one species in a restricted area has been found previously in the genus *Tethya* (Sarà et al., 1993), and similar analyses of genetic data and niche differentiation of the *Tethya* species at South Mole may find these colour morphs to also be distinctive at the species level.

TIMING OF REPRODUCTIVE DEVELOPMENT. The timing of reproductive activity in sponges has previously been related to sea temperature, with many species found to initiate activity as sea temperatures increase (Simpson, 1984 and references therein). Fewer studies have found sponges to be reproductively active as temperatures fall or are at a minimum. In the present study most sponge species were reproductive as sea temperatures were increasing or reaching their summer maximum (i.e. *Tethya* sp., *Chondrilla australiensis, Mycale* sp. and possibly *Echinodictyum clathrioides*). At this stage there is not enough information about the reproductive activity of *E. clathrioides* to say with certainty when release of reproductive products occurs. In contrast, two species commenced reproductive activity as sea temperatures were decreasing (i.e. *Coelosphaera* sp. and *Haliclona* sp.). *Haliclona* sp. appears to develop embryos and larvae throughout the winter.

Light regimes are another environmental factor that could influence onset of reproductive activity in sponges. Elvin (1976) found that initiation of oogenesis in the temperate intertidal species *Haliclona permollis* was most closely related to an increase in incident light. Ilan & Loya (1990) speculated that the reproductive activity of *Niphates* sp. may be related to the seasonal disappearance of algae, thereby increasing incident light to the sponges. At South Mole, biomass of the *Ecklonia* fringe appears to increase during the summer months when the photoperiod has increased, and may therefore increase shading of sponges.

A third exogenous factor implicated in the timing of reproductive activity is food availability (Sarà, 1992). The occurrence of two different periods of reproductive activity of sponges at South Mole may coincide with two peaks in the abundance of ultraplankton (A. Pile, Flinders University of South Australia, pers.comm.), one peak occurring in late summer/autumn when most of the species release their products, and a second peak in spring when reproductive products are released by *Haliclona* sp.

Two explanations are possible to explain these opposing trends in timing of reproductive activity: 1) species are responding to different environmental cues which trigger initiation of reproductive activity, or 2) species are responding differently to the same environmental cues.

SUMMARY

This study shows that modes of reproduction in sponges from South Mole, southern WA, conform to modes already documented in the literature for these respective genera. More work is required to unequivocally determine sex phenotype of these species, but preliminary data indicate that this aspect of their reproductive biology also appears to conform to the majority of reports in the literature. Reproductive activity in two of the species in autumn and winter is unusual, and possible reasons for this require further investigation. For the present, a baseline has been established in the timing of activity which will support future investigations on many other aspects of the reproductive biology of these species. Larval biology, diurnal timing of spawning for species that broadcast their products, and analysis of the partitioning of resources in species known to have both sexual and asexual reproduction, would all be useful studies. Species with colour morphs should be examined using genetic methods, or monitored for reproductive isolating mechanisms, to establish whether they are distinct species occurring sympatrically at the study site or if some other factors are responsible for their observed differences.

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